



Research papers

A general analytical approach for assessing the effects of hydroclimatic variability on fish habitat

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ABSTRACT

We propose a novel analytical approach that provides a simple, integrated tool for assessing the effects of hydroclimatically-driven flow regime variations on fish habitat. Average habitat quality metrics can be predicted effectively by an analytical equation. This is the result of the integration of two functions describing (a) the flow regime (the frequency distribution of discharge) and (b) the relationship between discharge and habitat quality. We applied this approach as a “proof of concept” to a simple model of velocity thresholds for juvenile salmon fry. The flow regime was described by a gamma distribution with physically meaningful parameters derived using a mechanistic-stochastic approach that explicitly links the flow regime to hydro-meteorological conditions and catchment wetness. Under different flow conditions, habitat quality was estimated using hydraulic habitat models. An empirical analytical function was then used to describe the relationship between specific discharge and habitat quality. Six river channel reaches characterized by different bed geometry and morphology were investigated. Four reaches are located in the Girnock burn, a natural upland river in the North of Scotland, while the remaining two reaches are located in the River Lyon in the central Highlands of Scotland that is heavily regulated for hydropower production. Results show that the stochastic model and the analytical function applied, each containing three parameters, successfully described Girnock (in both dry and wet years) and Lyon (naturalised) flow regimes and captured the relationship between available habitat and specific discharge reasonably well. For each site we obtained heat maps linking climatic and landscape features to bi-monthly average available habitat. These maps can provide clear generalised insights into the potential effects of hydroclimatic variations on metrics of fish habitat and have potential for wider applications using more complex habitat model.

1. Introduction

Freshwater ecosystems are particularly sensitive to hydroclimatic variability and the likely effects of climate change, and this has potential implications for aquatic organisms (Ormerod, 2009). Likely impacts may include changes to flow regimes (Poff and Zimmerman, 2010), increased water temperatures (Beechie et al., 2013), and water quality changes (Miserendino et al., 2011). The primary effects that variations in flow regime have on in-channel hydraulics, indexed by the

spatial and temporal distribution of water velocity, depth and wetted area, dictate that it is a key control on fish habitat (Ahmadi-Nedushan et al., 2006). Indeed, hydrological extremes of floods and droughts can have a significant impact on fish growth and mortality (Elliott et al., 1997).

The last decade has seen numerous attempts to assess the effects of hydroclimatic variability and climate change on flow variability and fresh water organisms, including salmonids. For example, in the Mink Brook, a tributary of the Connecticut River (New Hampshire), Nislow

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and Armstrong (2012) investigated the effects of high and low summer flow regime on 0+ age Atlantic salmon fry, linking flow regime to summer growth and finding that fish grew best in wetter summers. Lobón-Cerviá and Bradford, 2014 utilised long-term hydrologic and fish data to investigate the relationship between annual survival and recruitment of brown trout (*Salmo trutta*) with several environmental variables in contrasting sites of the Rio Esva (Spain). They demonstrated that annual survival and recruitment were equally maximised by intermediate discharge and that their relationships were well described by parabolic curves. Alternatively, Jensen and Johnsen (1999) in the River Saltdalselv, northern Norway, looked at the effects of high spring floods on both juvenile salmon survival and growth and discovered that in years with high peak spring floods salmon parr grew less, though for 1 year (or older) parr, mortality is not significantly affected by discharge peaks.

Climate change predictions and future hydroclimatic conditions, on which such predictions are based, are rather uncertain. This uncertainty is the consequence of several factors including: model errors, initial conditions, forcing errors, and the uncertainty linked to General Circulation Models (GCM) and to the downscaling method that is used to obtain predictions at a catchment scale (Chen et al., 2011; Capell et al., 2013; Haddeland et al., 2014; Van Schaeybroeck and Vannitsem, 2016). In fact, habitat models assessing climate change effects on fish populations often utilise, as inputs, very uncertain regional predictions where, in some cases, even the direction of change is not known (Bates et al., 2008; Goode et al., 2013). To assess the uncertainty related to climate change predictions, habitat models have been commonly applied to a set of most probable scenarios (e.g. Muñoz-Mas et al., 2016; Papadaki et al., 2016). However, as the number of scenarios is usually limited, these models are unable to provide catchment managers with understanding the uncertainties of climate change predictions in relation to current hydroclimatic variability fish are adapted to. In this context, more general methods, analytically linking the variability of hydroclimatic conditions with metrics of fish habitat quality could provide managers with an evidence base for conservation plans not simply relying on a few “most likely” scenarios but based on the context of known variability.

Probability-based models have been widely used to describe the distribution of hydrologic and climatic data (Botter et al., 2007; Husak et al., 2007). This has shown that certain types of probability distributions provide remarkably good fits for specific environmental variables. For example, the gamma distribution is often an appropriate descriptor for daily precipitation and discharge data, while a normal distribution might be good for describing the frequency distribution of daily air temperature data. In this context, we propose a parsimonious analytical approach that combines analytical functions describing river flow regimes based on a stochastic method proposed by Botter et al. (2007) and metrics of habitat quality which can be derived from detailed ecohydraulic surveys (e.g. Fabris et al., 2017; Buddendorf et al., 2017). The stochastic model has three parameters describing the hydroclimatic conditions and the effects of morphological and hydrological attributes on water routing at a catchment scale. These parameters allow an analytical description of the effects of hydroclimatic changes on flow regime. To characterise past flow regimes, parameters can be directly estimated based on climatic and landscape data (Botter et al., 2013).

A wide range of habitat models are available, and are variously used depending on species, life stage of interest, and available data (Acreman and Dunbar, 2004). In theory, any habitat model can be utilised and integrated with an appropriate function that approximates the relationship between habitat quality and discharge. In the study reported here, simple hydraulic models based on velocity thresholds for juvenile salmon were used as a “proof of concept” (e.g. Fabris et al., 2017; Buddendorf et al., 2017). Alternatively though, for a first screening, or when data are limited, general instream habitat models can be used as a first approximation to derive the discharge-habitat quality relationship

(Lamouroux and Jowett, 2005). The effects of hydroclimatic variations on average habitat quality can then be assessed by evaluating the effects that stochastic model parameters have on habitat. A more simple and intuitive, though equivalent, approach involves building heat maps relating meaningful flow regime statistics (e.g. mean flow and variability) with average habitat quality (as in the example we present). By analytically linking habitat quality to hydroclimatic variables and flow regime characteristics, such models can therefore provide general insights into the effects of hydroclimatic variations on in-stream habitat. The main advantage of such approach is that it can extend and generalise the results of hydraulic habitat models, and help managers who want to protect freshwater species from climate change effects to take more evidence-based decisions based on known hydroclimatic variations, independently of uncertain climate change predictions. Here, in our example of model application, we use salmon fry (*Salmo salar* L.), newly emerged from eggs in river gravels, as a target species due to its ecological and economic importance (Winfield et al., 2004; Walsh and Kilsby, 2007), but also because of the intolerance of this life stage to high flow velocities, which under high flow conditions may hinder feeding opportunities or cause fish to be swept away (e.g. Geist et al., 2000; Kynard et al., 2000; Mallet et al., 2000). Potential available habitat is used, in our example, as a very simple metric for habitat quality. Available habitat was derived by combining 2D hydraulic models with simple velocity threshold (the critical displacement velocity: CDV) above which fish cannot hold position and feeding opportunity and therefore fish growth may be limited (Graham et al., 1996). Specifically, the aims of this paper are to: 1) show how a mechanistic stochastic-model, based on physically-based parameters that depend on hydroclimatic and catchment conditions, can successfully describe both variable, or “erratic”, and persistent, or “stable”, flow regimes; 2) describe how analytical functions can be used to conceptualise the relationship between discharge and metrics of habitat quality; and 3) provide a simple, integrated and generalized approach to assessing the effects of hydroclimatically-driven flow regime dynamics based on a metric of fish habitat quality. As a “proof of concept”, the method is here applied to investigate the effects of hydroclimatic variations in terms of flow regime on Atlantic salmon fry in six contrasting river reaches in the Scottish Highlands.

2. Study site

Overall, we investigate six reaches (Fig. 1). Four reaches are located in the Girnock Burn, a small, undisturbed long-term salmon monitoring stream known to provide extensive suitable habitat for juvenile salmon (Glover et al., 2018). The remaining two reaches are located in the heavily regulated River Lyon, a larger tributary of the River Tay, Scotland's largest river system (Birkel et al., 2014).

For the Girnock sites, the catchment, is dominated by heather (*Calluna vulgaris* and *Erica tetralix*) moorland with some Scots Pine (*Pinus sylvestris*) forests only in the lower part of the catchment; which has an area of about 32 km² and ranges in altitude from 230 to 862 m a.s.l. (Gibbins et al., 2002). Catchment geology is mainly characterized by granite and calcareous schist which is overlain by glacial drift deposits in the valley bottom. Soils are dominated by organic rich peaty soils in the riparian area. Mean air T is ~6.3 °C with annual precipitation, relatively evenly distributed throughout the year, of ~1000 mm of which less than 10% falls as snow. The main stem is ~9 km long with an average slope of 0.029 (Moir et al., 1998) and the channel bed is dominated by step-pool and plane beds (Moir et al., 2006). The mean daily discharge, measured ~200 m upstream of the catchment outfall, is ~0.53 m³ s⁻¹ (0.14 cm d⁻¹) with peaks > 8 m³ s⁻¹ (2.3 cm d⁻¹).

The investigated reaches, which are extensively described by Fabris et al. (2017), going from upstream to downstream are: Iron Bridge (IB), Hampshire's Bridge (HB), Diagonal Fence (DF), and Forest Automatic Weather Station (FAWS) (Fig. 1). IB, HB and DF are moorland sites with

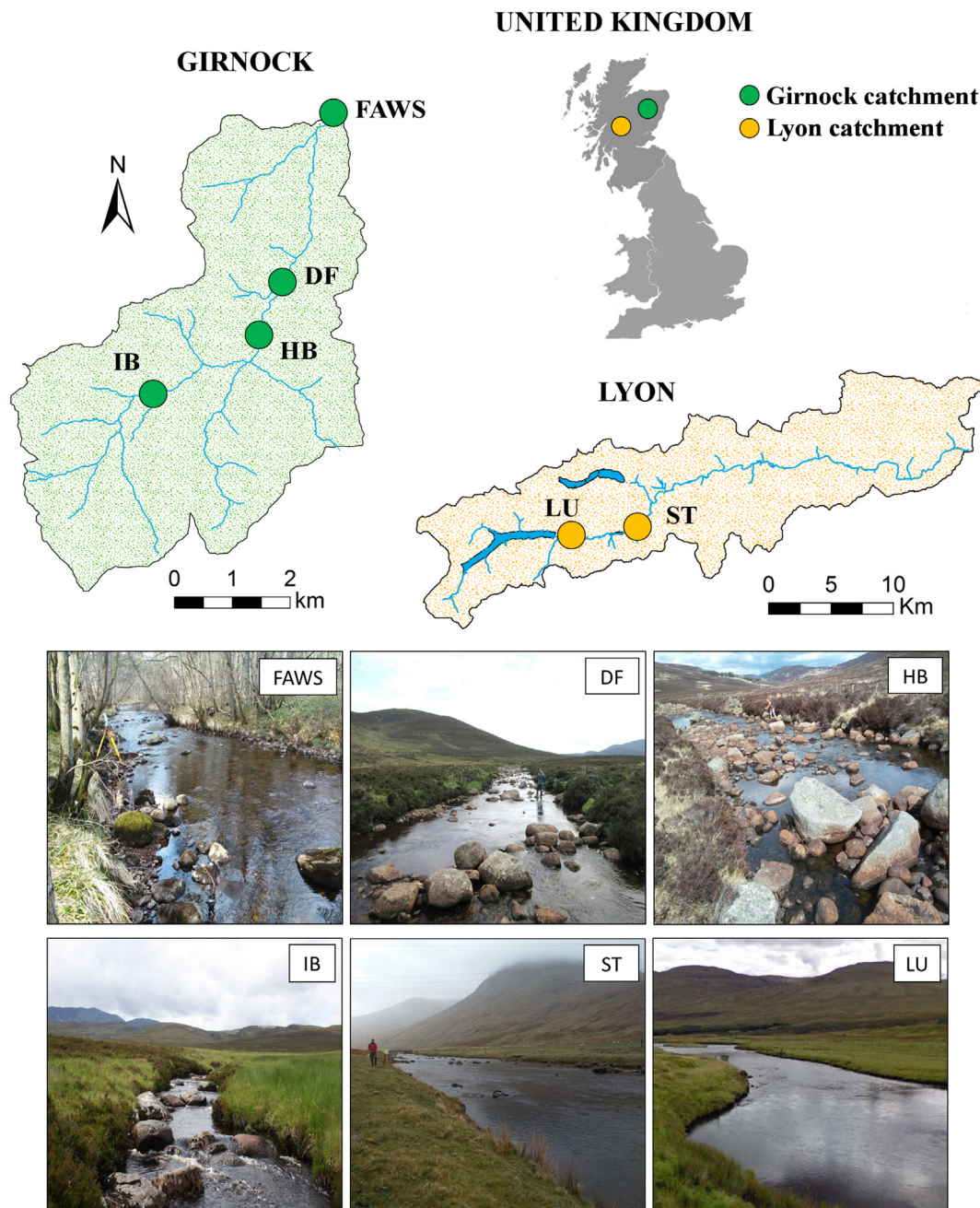


Fig. 1. Girnock and Lyon catchments and their locations in the UK map. Girnock Burn sites: Forest Automatic Weather Station (FAWS), Diagonal Fence (DF), Hampshire's Bridge (HB), and Iron Bridge (IB). Lyon sites: Stronuich (ST), and Lubreoch (LU).

undercut banks and the riparian vegetation is dominated by heather shrubs, while FAWS is a forest site with well-defined banks.

The remaining 2 reaches, Lubreoch (LU – upstream) and Stronuich (ST – downstream) [Fig. 1](#), are located along the Lyon River, a highly regulated tributary of the river Tay in central Scotland utilised for hydroelectric power production since 1958 ([Geris et al., 2015](#)). The Lyon catchment has an area of 391 km² that ranges from 92 to 1192 m a.s.l. and its land cover is dominated by moorland with some patches of forest distributed along the river. The mean annual precipitation is ~2290 mm (more than twice that of the Girnock burn) is evenly distributed throughout the year. In winter time a large portion of the precipitation falls as snow especially at the higher elevations ([Geris et al., 2015](#)). Air temperature ranges from –15 to 25 °C. The river length is ~49 km and has a mean discharge of ~12.5 m³ s^{–1} (0.28 cm d^{–1}) measured at the outlet section of the catchment.

The Lyon sites are extensively described by [Buddendorf et al. \(2017\)](#). LU and ST are both characterized by a flat plane bed with the presence of some large roughness elements. Banks are covered by grass with no presence of trees or shrubs.

The geometry (longitudinal length and width), the slope, and the roughness of all the sites investigated are reported in [Table 1](#). Bathymetric surveys of each site and their detailed characteristics are described by [Fabris et al. \(2017\)](#) (Girnock) and [Buddendorf et al. \(2017\)](#) (Lyon). Average site width was calculated by dividing the wetted area by its length under mean discharge conditions (mean daily discharge recorded and scaled for each site in proportion to its drainage area). Slope has been calculated as the average slope of the water surface while roughness was computed as a detrended standard deviation of bed bathymetry using TopCAT tool ([Olsen et al., 2012](#)).

Table 1

It reports for each of the Girnock and Lyon site investigated the slope (a mean value for each site), the roughness, the longitudinal length, and the mean width (estimated under mean discharge).

	Girnock			Lyon		
	IB	HB	DF	FAWS	LU	ST
Slope [–]	0.022	0.021	0.011	0.003	0.003	0.003
Roughness [m]	0.124	0.112	0.078	0.068	0.028	0.028
Length [m]	76.3	30.5	17.5	16.2	48.1	50.6
Mean width [m]	3.2	6.8	7.8	7.0	22.8	29.4

3. Method

For our purposes, the flow regime is defined as the frequency distribution of river flows for a particular period of interest, which can be described using a gamma distribution according to the stochastic model proposed by Botter et al. (2007, 2013). The version of the model that we utilised contains three parameters, that are not simply calibrated against observations, but are explicitly related to climatic and catchment conditions allowing a direct linkage of the flow regime variation to rainfall inputs and catchment wetness conditions. For the current study, we defined the flow regime for the fry post-emergence period (May–June). A second analytical function is then utilized to relate the habitat availability (metric of habitat quality for our example) to specific discharge. This relationship is based on habitat availability produced by detailed hydraulic modelling described fully by Fabris et al. (2017). Parameters in this case are calibrated against simulated values and do not have clear physical meaning. Hence, an average value of the available habitat for the period of interest is obtained integrating the product between these two functions. In the case, we focus on a simple metric for fry habitat, but the approach is generic and can be used with any other habitat models dependent on flow.

3.1. Flow regime $p(q)$

The flow regime for the post-hatch period (May–June), which is one of the most flow-sensitive periods for newly-emerged, small juvenile salmon fry (average length of fry caught in the Girnock during electrofishing ~ 4.8 cm), is represented by a probability density function according to a mechanistic stochastic-model in which streamflow (q [$L T^{-1}$]) dynamics are assumed to be driven by a catchment-scale soil–water balance forced by stochastic daily rainfall inputs (Botter et al., 2007).

In this context, runoff events result from the modulation of daily rainfall inputs according to the antecedent wetness of the catchment soils. Rainfall is modelled as a spatially uniform marked Poisson process with mean depth α [L] and mean rainfall frequency λ_p [T^{-1}]. Although α quantifies the average daily intensity of rainfall events, the runoff frequency λ is smaller than the underlying precipitation frequency λ_p because any soil–water deficit created by evapotranspiration (ET) in the rooting zone needs to be satisfied before water is routed to streams. Effective rainfall is consequently modelled as a spatially uniform marked Poisson process with mean depth α [L] and mean runoff frequency λ [T^{-1}]. Therefore, λ , by accounting for the ET crucially embeds rainfall attributes, soil/vegetation properties, and other hydroclimatic variables, such as temperature, humidity, and wind speed.

The time scale of the hydrological response, defined as the mean

water retention time in the upstream catchment, is operationally identified by the inverse of the recession constant k [T^{-1}] observed during recessions, conveniently assumed to be exponential. This allows simulation of the slow release of water from the soil and underlying aquifers to assume that the entire catchment is modelled as a linear reservoir (Botter et al., 2007). The term k quantifies the effect of catchment-scale morphological and hydrological attributes controlling water routing. High k values imply low duration of the flow pulses released from the catchment after rainfall, typical of fast-responding catchments. The shape of the distributions is determined by the ratio λ/k . We distinguished between erratic (dry) and persistent (wet) flow regimes. Erratic flow regimes are characterized by exponentially shaped frequency distributions with high frequencies for very low flows that monotonically decrease with q ($\lambda/k < 1$), while persistent conditions are characterized by bell shaped frequency distributions with an increase of frequency with q until a maximum after which frequencies begin to decrease increasing q ($\lambda/k > 1$).

The model allows an analytical expression of the streamflow probability distribution $p(q)$ (Botter et al., 2007):

$$p(q) = \frac{(\alpha k)^{-\frac{\lambda}{k}}}{\Gamma(\lambda/k)} q^{\frac{\lambda}{k}-1} \exp\left(\frac{-q}{\alpha k}\right) \quad (1)$$

That can be written:

$$p(q) = \frac{(\mu CV^2)^{-CV^2}}{\Gamma(CV^2)} q^{CV^2-1} \exp\left(\frac{-q}{\mu CV^2}\right) \quad (2)$$

With:

$$\mu = \alpha \lambda \quad (3)$$

$$CV = \sqrt{\frac{k}{\lambda}} \quad (4)$$

where μ is the mean and CV is the coefficient of variation of the specific discharge. CV , also known as relative standard deviation represents a standardized measure of dispersion of a probability distribution around the mean. Table 2 shows the ranges of the parameters for the Girnock and the Lyon respectively.

3.2. Available habitat $AH(q)$

The spatial distribution of water depth and velocity, and therefore the available habitat (AH), in river channels are largely determined by the interactions of q and bed morphology (Leopold and Maddock, 1953). In this example to determine AH under different q , we utilized a simple approach based on a critical displacement velocity index (CDV), which represents a velocity threshold above which juvenile salmon are unable to hold station and fish feeding activity may be impeded (Tetzlaff et al., 2005). CDV depends upon fish size and stream temperature and was empirically defined through laboratory experiments (Graham et al., 1996) as a function of water temperature (T [$^{\circ}C$]) and fish size (L [m]). CDV for salmon fry is defined:

$$CDV = (4.14 \log(T)) + 1.74) L \quad (5)$$

Considering that the scope of our example is to study the effects of hydroclimatically-driven flow regime variations in sites characterized by different bed morphology and geometry, for simplicity, we fixed values for both T (11.5 $^{\circ}C$ – the mean water temperatures for May–June period from 2007 to 2011 recorded at the HB site) and L (0.046 m – the

Table 2

Mechanistic stochastic model parameter ranges for the Girnock and Lyon catchments.

	α [cm]	λ_p [d^{-1}]	λ [d^{-1}]	k [d^{-1}]	μ [cm d^{-1}]	CV [–]
Girnock	0.09–0.52	0.49–0.90	0.11–0.57	0.11–0.59	0.01–0.22	0.64–1.96
Lyon	0.27–1.04	0.66–0.85	0.29–0.62	0.18–0.32	0.08–0.64	0.71–0.77

average length of fry in the Girnock during electrofishing surveys), obtaining a CDV equal to 0.29 m s^{-1} . This was then used to define areas where fry habitat was either present or unavailable.

For the investigated sites, 2D hydraulics models were built to obtain spatial distributions of the average water column velocity under different flow conditions. For each flow condition, velocity spatial distributions were then combined with CDV to obtain the *AH* (area where water velocity was below CDV). A similar process is described in detail for salmon parr by Fabris et al. (2017). Of course we recognise that this is a simplification and conservative estimate of fry habitat availability as fry can hold station on the stream bed and use short swimming bursts in foraging. Nevertheless, it provides a simple habitat metric to test the approach with. Finally, for each site we used an analytical function to fit the estimated available habitat. The distribution of the available habitat estimations suggests that these can be relatively well approximated by an exponential function with three parameters:

$$AH(q) = C \exp(-Bq) q^{A-1} \quad (6)$$

where the parameters (A [–], B [L T^{-1}], and C [T L^{-1}]) depend on bed geometry and morphology, and CDV (water temperature and fish length).

For each site the parameters were simply calibrated against values estimated from combining hydraulic models with the CDV threshold, according to the non-linear least squares method (Johnson and Faunt, 1992). Theoretically any other function could be chosen. However a key point is to find a good trade-off between the fit of data and the complexity of the function. Since *AH* is site size dependent, for each site in order to allow site comparisons, *AH* was normalized by the wetted area (*WA*) estimated for each site under mean flow conditions.

3.3. Average available habitat $\langle AH \rangle$

To quantify the capacity of the investigated sites to provide usable habitat for newly emerged fry under different flow regimes, we consider an average value of the available habitat ($\langle AH \rangle$ [L^2]) for the period of interest (May–June). The analytical expression of $\langle AH \rangle$ can be obtained by integrating the product between $p(q)$ and $AH(q)$:

$$\langle AH \rangle = \int_0^\infty p(q) AH(q) dq \quad (7)$$

Using Eqs. (1) and (6), $\langle AH \rangle$ can be written as:

$$\langle AH \rangle = \frac{C(\alpha k)^{A-1}}{(1 + B\alpha k)^{A+\lambda/k-1}} \frac{\Gamma(A + \lambda/k - 1)}{\Gamma(\lambda/k)} \quad (8)$$

Using Eqs. (3) and (4), Eq. (8) can be expressed as a function of mean discharge (μ) and coefficient of variation (CV) as:

$$\langle AH \rangle = \frac{C(\mu CV^2)^{A-1}}{(1 + B\mu CV^2)^{A+CV^{-2}-1}} \frac{\Gamma(A + CV^{-2} - 1)}{\Gamma(CV^{-2})} \quad (9)$$

Again $\langle AH \rangle$ was normalized by *WA* to allow comparisons among sites.

4. Results

4.1. Mechanistic stochastic model $p(q)$

Fig. 2 shows examples of the distribution of specific discharge observations, measured at the outlet of the catchment (blue bars) against the analytical probability density functions estimated using the mechanistic stochastic model (red lines) for the Girnock Burn for two contrasting years. The mechanistic stochastic model adequately captures the frequency distribution of flow observations both under erratic – dry (1974, Fig. 2) and persistent – wet conditions (1983, Fig. 2), with an average error between modelled and observed 0.2, 0.5, and 0.8 quantiles equal to 0.021, 0.022, and 0.014 cm d^{-1} respectively. For the erratic flow (persistent) regime mean daily specific discharge remains

below 0.4 cm d^{-1} (1 cm d^{-1}), with higher frequencies occurring for $q < 0.15 \text{ cm d}^{-1}$ (0.4 cm d^{-1}).

Fig. 3 shows the specific discharge distributions against the analytical probability density functions for the River Lyon for the years 2010 and 2011. As previously noted, since the 1950s the River Lyon has been regulated with flows controlled by reservoir releases. Consequently, it was not possible to obtain specific discharge distributions directly from observations and naturalised flow regimes had to be simulated by a rainfall-runoff model based on the HBV modelling framework (Geris et al., 2015). Even in this case, the model successfully captured the flow regime for the fry emergence period, even though we could test the stochastic model only under persistent (i.e. wet) conditions. Modelled and observed 0.2, 0.5, and 0.8 quantiles differ of 0.030, 0.007, and 0.095 cm d^{-1} respectively. For the less persistent (i.e. close to erratic) flow regime in 2010, mean specific daily discharge remains below 0.4 cm d^{-1} with higher frequencies occurring for $q < 0.15 \text{ cm d}^{-1}$, while for the more persistent flow regime in 2011, frequencies are relatively uniformly distributed with q remaining below 1.2 cm d^{-1} .

4.2. Analytical habitat availability $AH(q)$

Fig. 4 shows the modelled *AH* for a given specific discharge obtained for the four Girnock Burn (Fig. 4a) and the two Lyon (Fig. 4b) sites by combining hydraulic models and CDV assessment and normalizing by the *WA*. The relationship between *AH*/*WA* and q shows the same bell-shaped pattern for all the 6 sites, even if this is less pronounced for the 2 Lyon sites where the bell is compressed against the y-axis. *AH*/*WA* is quite high under relatively low flow where we can find a maximum after which it monotonically decreases to values close to 0 in correspondence of relatively high q (≈ 1 and 0.4 cm d^{-1} for the Girnock and Lyon sites respectively). Lines show the equivalent relationship described by the functions that we used to describe analytically the dependence of *AH* from q . The exponential function with three parameters (with no physical meaning) provides an adequate fit to the data with R-square ranging between 0.984 (ST) and 0.995 (FAWS).

4.3. Generalised integrated model

As previously observed, the flow regime during the period around and soon after fry emergence is well reproduced by gamma distribution that can be simply defined by mean specific discharge μ and the coefficient of variation CV that the mechanistic stochastic model used explicitly relates to mean rainfall depth α , mean runoff frequency λ and the inverse of the flow recession constant k . Effects of flow regime on $\langle AH \rangle$ can be therefore investigated either analytically, using equation (9) or equivalently by building heat maps that show $\langle AH \rangle$ for different combinations of μ (αk) and CV ($\sqrt{k/\lambda}$).

Accordingly, Figs. 5–7 show how $\langle AH \rangle$ normalized by *WA* varies under different flow regime conditions (simply defined in terms of the statistics μ and CV) for the six investigated sites. As the $AH(q)$ functions have broadly similar shape for all the sites apart from LU, even with different absolute values, $\langle AH \rangle$ shows the same pattern between these sites (Fig. 6).

To show the general behaviour of $\langle AH \rangle$, Fig. 5 considers values of μ and CV ranging between 0 and 3 cm d^{-1} , and 0 and 6 cm d^{-1} respectively, covering most of the existing persistent and erratic hydroclimatic settings (Botter et al., 2013). Values of the normalised *AH* range between 0 and 0.8. In the maps, we can see the presence of parallel bell-shaped (lines with constant *AH*/*WA*) (for the five sites with similar $AH(q)$) and exponentially shaped (for LU) contour lines, developing respect to the y-axis showing how different flow regimes can provide on average the same *AH*/*WA*. The position of the maximum with respect to the y-axis of these curves depends on the shape of the $AH(q)$ function. This results in Girnock Burn (bell shaped $AH(q)$) sites providing, in general, more usable habitat under persistent or slightly erratic flow regimes. In contrast, the Lyon (almost exponential $AH(q)$)

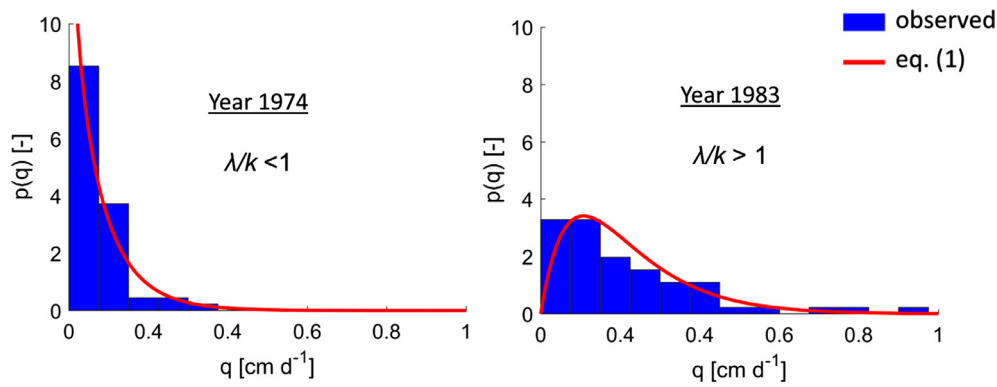


Fig. 2. For the Girnock Burn, examples of frequency distributions of discharge observations (May–June) and analytical pdfs obtained by using the stochastic model for 2 contrasting year: one erratic (left) and one persistent (right).

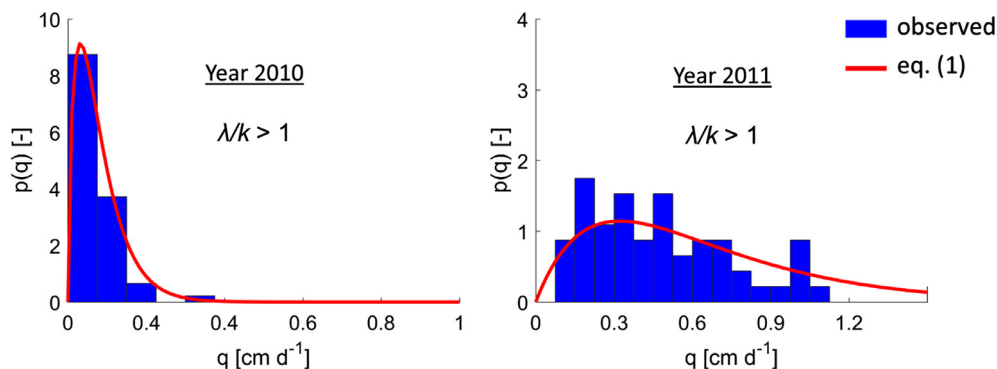


Fig. 3. For the Lyon, examples of frequency distributions of discharge (May–June) obtained by model simulations and analytical pdfs obtained by using the stochastic model. In this case there was not erratic year (2010 was quite close though) but only persistent.

sites tend to provide more usable habitat under very erratic flow regimes. The dispersion of these curves is proportional to the variance of $AH(q)$.

Fig. 6 highlights the CV that maximizes $\langle AH \rangle$ for each value of μ and vice versa for the different sites. According to the first part of the curves (low μ) we have relative maximum of $\langle AH \rangle$ in correspondence of CV close to 0. Then for higher values of μ , the CV that maximizes $\langle AH \rangle$ logarithmically increases with μ . This dictates that while under low flow regimes (low μ) $\langle AH \rangle$ is maximised by stable flows, under wetter conditions (higher μ) more variable flow regimes can provide greater values of $\langle AH \rangle$. As we previously noted, the positions of $\langle AH \rangle$ relative maximum is strictly related to the position of the maximum in the $AH(q)$. Clearly the higher the q that maximizes $AH(q)$, the lower the CV that maximize $\langle AH \rangle$ for a fixed q .

Furthermore, the plot demonstrates that streamflow variability is a critical hydrologic attribute with potentially important implications for river ecosystems; and that for many sites and hydrological conditions, a certain degree of flow variability is necessary to maximise the habitat availability.

Fig. 7 summarizes the response of $\langle AH \rangle / WA$ for more constrained values of μ and CV for the prevailing low flows during the post-emergence period for the Girnock burn. Grey dots show the statistics of each annual flow regime (May–June) observed from 1972 to 2011 while red and blue dots respectively correspond to the erratic (1974) and persistent (1983) years reported in Fig. 2. The erratic year is characterised by a higher CV and a smaller μ with respect to the persistent one. The plot shows how changes in $\langle AH \rangle$ are the result of simultaneous variations on both μ and CV. DF for the Girnock burn and

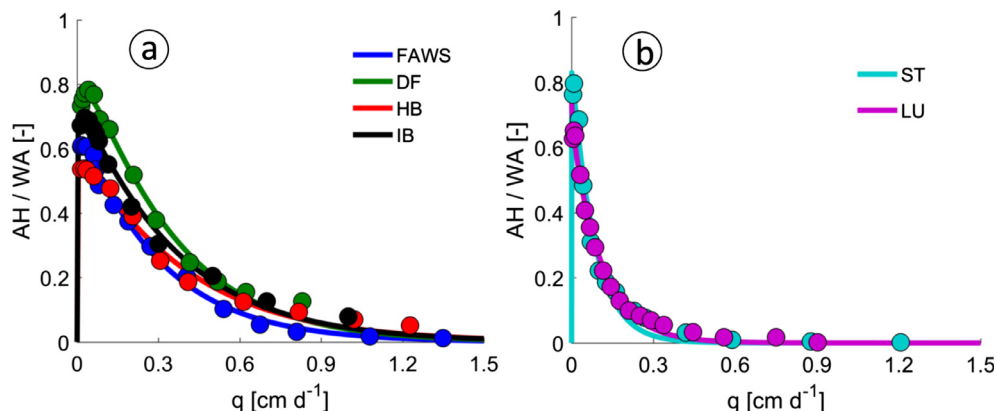


Fig. 4. Simulated normalized available habitats for fry as a function of discharge (dots) and corresponding analytical functions (lines) for Girnock (a) and Lyon (b) sites.

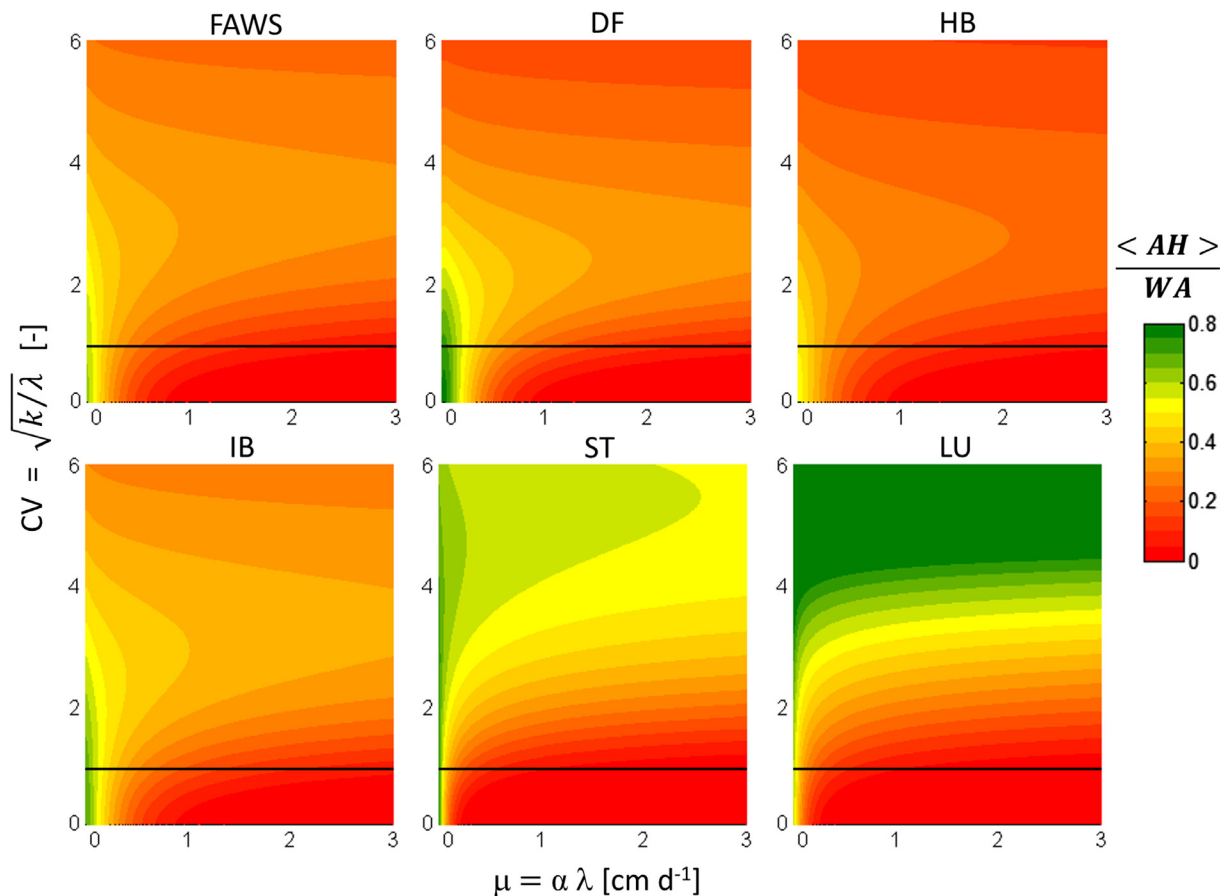


Fig. 5. General behaviour of normalized available habitat ($\langle AH \rangle / WA$) against arbitrary values of mean discharge (μ) and coefficient of variation (CV). Each combination of μ and CV identifies a specific flow regime.

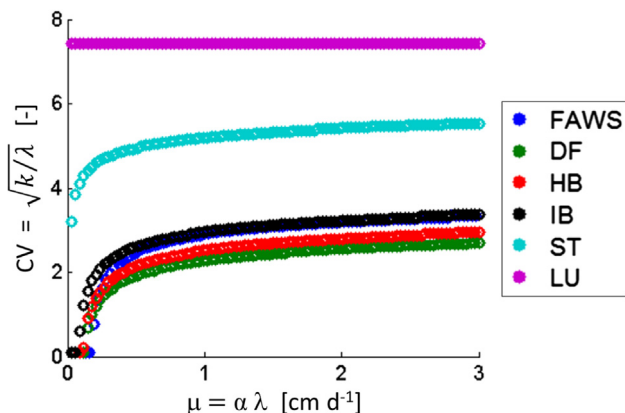


Fig. 6. Coefficient of variation (CV) that maximizes the available habitat (AH) for each mean discharge (μ).

ST for the Lyon give the higher values of $\langle AH \rangle / WA$ for the entire domain with peaks of $\langle AH \rangle / WA$ around 0.8. The lowest values of $\langle AH \rangle / WA$ for the Gironck sites, around 0.3, occur in DF, while the lowest values for the Lyon sites, about 0.1, occur in ST in correspondence of $CV > 2.7$ and $\mu = 0.2$. The remaining 3 sites (FAWS, IB, and LU) are more moderate with less extreme values of $\langle AH \rangle / WA$. Considering flow regimes characterised by similar μ , DF and HB show a decrease in $\langle AH \rangle / WA$ with flow regime moving from persistent (wet, $CV < 1$) to erratic (dry, $CV > 1$), (1974 vs. 1983). In contrast, ST and LU show an increase in $\langle AH \rangle / WA$ in correspondence of the persistent-erratic transition area (1974 vs. 1983), while FAWS and IB are not characterised by any significant variations (1974 vs. 1983). The

heterogeneous pattern of $\langle AH \rangle / WA$ among different sites shown in Fig. 7 can be related to inter-site differences in the effect of μ and CV on habitat availability. While increasing μ generally leads to reduced $\langle AH \rangle$, $\langle AH \rangle$ can either increase or decrease with CV depending on the shape of the function $AH(q)$, which is related to site morphology and hydraulics.

To analyse the effect of mean specific discharge and streamflow variability on habitat quality, Fig. 8 shows the pattern of $\langle AH \rangle / WA$ for the post-emergence period for the Lyon during four consecutive springs (May–June) in the period 2008–2011 with red and blue dots corresponding to the persistent years (2010, 2011) reported in Fig. 3. The plot shows a systematic decrease of $\langle AH \rangle$ with increasing μ . Here, Gironck sites are by far the best sites with values of $\langle AH \rangle / WA$ that go up to 0.8. For the Lyon sites, ST seem to be slightly better even if both site have very low $\langle AH \rangle / WA$ (around 0) for persistent flow regime ($CV < 1$) with $\mu > 0.2$.

5. Discussion and conclusion

In this paper, we have proposed an analytical approach where a simple metric of fish habitat quality is directly and explicitly linked to hydroclimatic variables and catchment conditions that can define the flow regime for a period of ecological interest. The model is the result of two functions describing the flow regime and the relationship between discharge and habitat quality. A key element is the mechanistic stochastic model proposed by Botter et al. (2007) which allows us to explicitly link hydroclimatic and catchment characteristics, described by physically meaningful parameters, to flow regime. Compared to standard rainfall runoff models, the mechanistic stochastic model here adopted has the advantage of requiring a minimal amount of data and

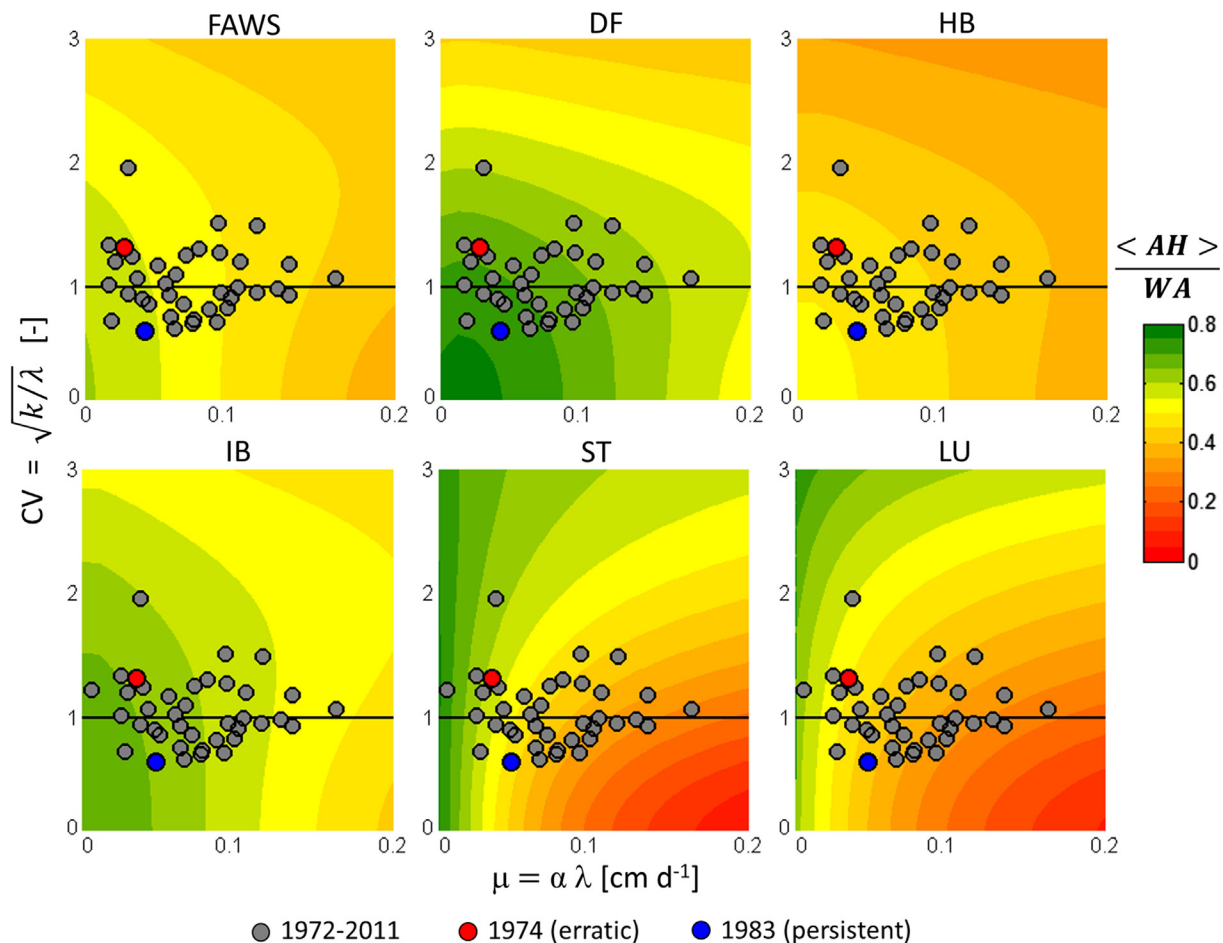


Fig. 7. General behaviour of normalized available habitat ($\langle AH \rangle / WA$) against arbitrary values of mean discharge (μ) and coefficient of variation (CV) (more realistic ranges from Fig. 5). Each combination of μ and CV identifies a specific flow regime. Dots represent flow regimes observed in the Girnock from 1972 to 2011 (May–June). Red and blue dots correspond to the erratic (1974) and persistent (1983) years reported on Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

using parameters that can be assessed exclusively based on climatic and landscape data (and discharge data in this specific case) requiring in principle no calibration against discharge time series. Confirming the positive results obtained by Botter et al. (2010, 2013), Basso et al. (2015), and others, who successfully used the stochastic model to analytically describe the flow regime in different catchments in Italy, Swiss and the US, the example reported here underlined the consistency of this mechanistic stochastic model in reproducing the flow regime in both erratic (dry) and persistent (wet) conditions. It is reassuring that the model can do this even in challenging conditions such as this, where parameter estimation has to be based on a limited number of observations (e.g. a 61 day period in May–June). Since it performs equally well, the linear version of the model (3 parameters) has been preferred with respect to the alternative non-linear version (4 parameters) that can consider several stages of recession and be applied to more complex flow regimes (Botter et al., 2009).

“As a proof of concept”, in our example we utilized rainfall and specific discharge observations or simulations, for the May–June period, to estimate parameters α , λ , and k . However, Doulatyari et al. (2015) showed alternative ways, based on catchment morphology, stream network and potential evapotranspiration, which do not require discharge observations or simulations to determine λ and k parameters. In our case, it seems that the analytical function chosen is adequate to describe the relationship between available habitat and specific discharge. This function includes the effects of bed morphology on in-reach hydraulics and it is therefore site specific. This implies that the

modelling approach can be transferred to other catchments, but this function should be calibrated to the specific sites. However similar sites have similar curves that might be used as first approximation for particular river reach morphologies. Our results showed how $AH(q)$ curves were relatively similar for each river. On the other hand, the curves diverged substantially between the Girnock and Lyon due to significant differences of slope, roughness, and geometry between the two rivers.

The effects of flow regime variability and change (due to hydroclimatic difference, climate change or changes in land use) on fish habitat have been the focus of many studies in the last decade (Jonsson and Jonsson, 2009; Wenger et al., 2011). Hydraulic habitat models are the most common approaches that have been utilised to assess the effects of flow regime alteration on fish habitat (Ahmadi-Nedushan et al., 2006; Dunbar et al., 2012). These include simple threshold models (Fabris et al., 2017), semi-quantitative approaches (e.g. PHABSIM; Gard, 2009; Gibbins et al., 2002), presence-absence models (e.g. Scott et al., 2005), fuzzy models (e.g. Mocq et al., 2013), and multivariate statistical methods (e.g. generalised additive models, GAMs; Buddendorf et al., 2017; Millidine et al., 2012). However, despite their complexity, all these models are applied to a restricted number of climate change scenarios that are affected by a high degree of uncertainty, especially at a catchment scale (Chen et al., 2011; Murphy et al., 2010). In this context, combining results from various kinds of hydraulic habitat models with the analytical flow model proposed here, we can overcome this issue, and provide a more general approach, explicitly showing the effects of hydroclimatic variability (e.g. mean rainfall) on various

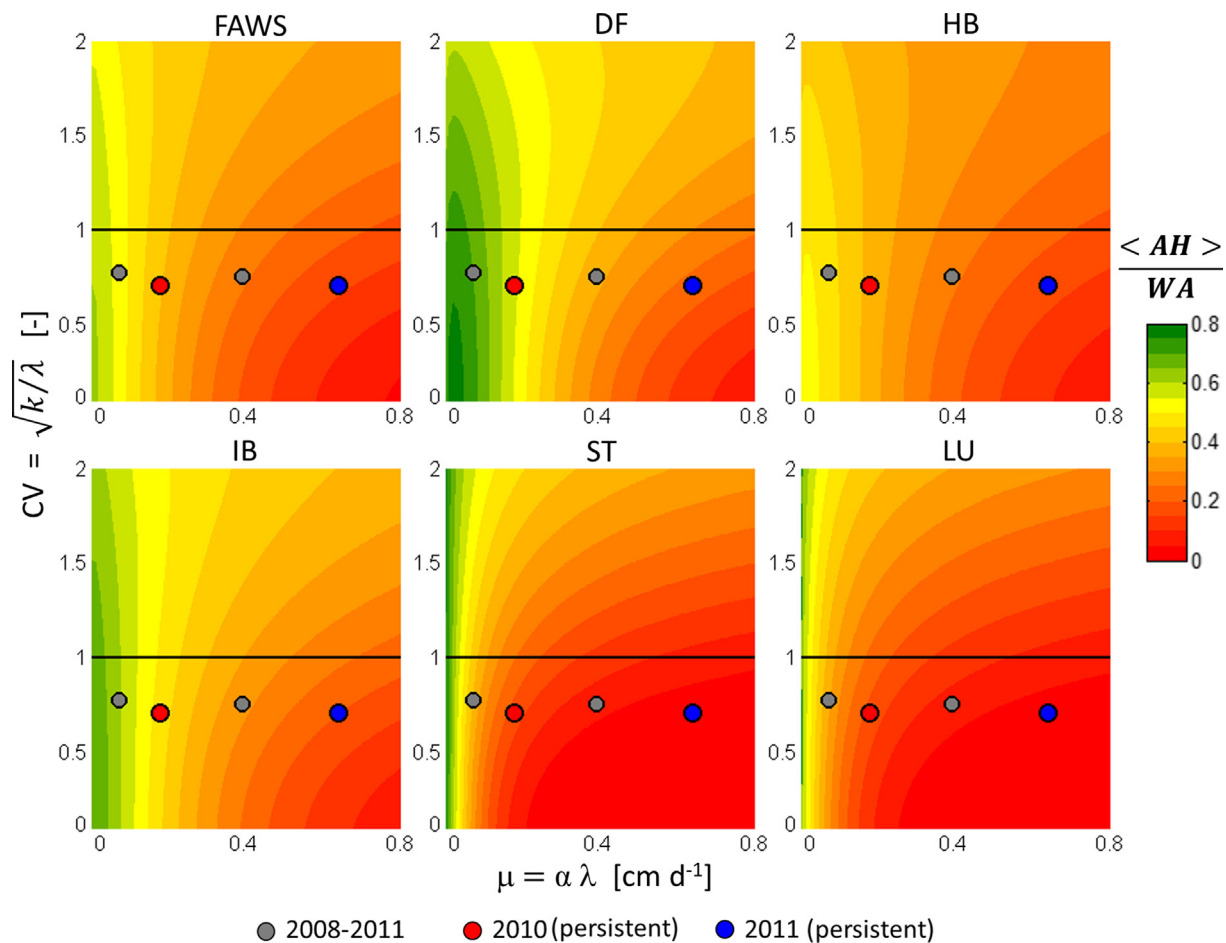


Fig. 8. General behaviour of normalized available habitat ($\langle AH \rangle / WA$) against arbitrary values of mean discharge (μ) and coefficient of variation (CV) (more realistic ranges from Fig. 5). Each combination of μ and CV identifies a specific flow regime. Dots represent flow regimes simulated for Stronach from 2008 to 2011 (May-June). Red and blue dots correspond to the persistent years (2010, 2011) reported on Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

habitat indices. Therefore, even without directly addressing uncertainty, compared to more commonly used approaches, this method has the advantage of providing valuable information about the effects of hydroclimatic alterations on habitat conditions regardless of uncertain climate change predictions. The effects of single or combined parameters (representing different hydroclimatic conditions) on the habitat quality can then be investigated by an analytical study of the equation or by analysing graphical maps (see Fig. 5 as an example).

A key advantage of this new analytical approach is that it clearly shows how simple maps can provide useful insights to visualise and assess the potential impacts that flow regime variations (therefore hydroclimatic factors and catchment conditions) could have on available habitat in sites characterised by different morphology and geometry. In particular, our results suggest that habitat is strongly influenced by the interplay of mean specific discharge and stream flow variability. Under flow regimes characterised by low mean specific discharge (a few mm d^{-1}), available habitat is maximised by low variability, while flow regimes characterised by greater mean specific discharge (which is more common and also necessary to sustain smolt migration in this period (Thorstad et al., 2012)), require a certain degree of variability to maintain high levels of available habitat. Therefore, flow regimes characterised by intermediate mean specific discharge and a certain degree of flow variability seem to be the best compromise to simultaneously sustain salmon flow requirements at different life stages. In line with the natural flow regime paradigm (Poff et al., 1997), this results further emphasises the importance, in regulated catchments, of management policies that maintain a certain degree of flow variability in

order to sustain riverine ecological functions.

However, although we recognise that the example presented here is a simple “proof of concept”, it provides a clear guide of how the modelling approach can be implemented, and the information that this method can provide. We should stress that we are well aware of the limitations introduced by assessing habitat availability for salmon fry based only upon a velocity threshold (CDV). In fact, other abiotic and biotic factors such as water depth, substrate and cover can also significantly influence salmon fry habitat availability. However, the use of more complex hydraulic habitat models including the effects of other variables, for instance water depth (not based only on CDV), are equally amenable to use with the approach described. Furthermore, by considering mean water column velocity, we are likely producing a conservative estimate of habitat availability as water velocity tends to follow a logarithmic profile with depth (Vito and Giorgio, 1994). This implies that, even when mean velocity is too high, fish can still rest in the proximity of the river bed where velocities are much lower (Höjesjö et al., 2015). In fact, it has been shown that juvenile salmon can spend time close to the river bed using pectoral fins for stability (Arnold et al., 1991), moving into the water column for short periods for foraging (Höjesjö et al., 2015). Instead, a limitation of the general 2-D hydraulic modelling approach is that it estimates an average daily quality of the habitat for the entire period of interest (May-June in our example). The importance of this simplification is probably strongly related to site characteristics, and life stage and species investigated. In fact, while some studies demonstrated that the habitat used by juvenile salmon was not substantially affected by short-term discharge fluctuations

(Berland et al., 2004; Robertson et al., 2004), others showed that in some situations, single extreme events can have greater impacts on fish density and distribution and therefore on habitat quality than more moderate conditions (Jensen and Johnsen, 1999). The latter can be theoretically incorporated by adding analytical weight functions to the model, but this is beyond the scope of the current study.

In conclusion, considering the high uncertainty on future hydroclimatic conditions especially at a catchment scale, we argue that the simple general integrated model proposed in this paper can be successfully combined with commonly used hydraulic habitat models to help river managers to take informed decisions that effectively maintain or improve freshwater habitat based on known hydroclimatic variability.

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